RESEARCH ARTICLE

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Might Flowers of Invasive Plants Increase Native Bee Carrying Capacity? Intimations From Capitol Reef National Park, Utah

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ABSTRACT: We compared the native bees visiting the flowers of three species of invasive plants, saltcedar (*Tamarix* spp.) and white and yellow sweet clover (*Melilotus albus*, *M. officinalis*), with those visiting seven concurrently blooming native plant species in mid-summer at three sites in Capitol Reef National Park, Utah. Overall, as many total species of bees visited the flowers of the three invasive plant species as visited the seven natives. On average, invasive species were visited by twice as many bee species as were natives. With a single exception, visitors of invasives were generalist bees, rather than specialists. *Colletes petalostemonis*, the only native legume specialist recorded, was an abundant forager on the flowers of both species of *Melilotus,* demonstrating that at least some specialist bees will move to invasive plants that are closely related to their usual hosts. Species abundant on the flowers of invasives tended to collect both pollen and nectar, suggesting that bees are using pollen of *Tamarix* and *Melilotus* to provision their offspring. We argue that invasives with entomophilous flowers are unlikely to either facilitate the reproduction of uncommon native plants or consistently compete with them for pollinators. Rather, they are likely, over time, to selectively increase the carrying capacity and population size of native bees, specifically generalists, and specialists of closely related plant species.

Index Terms: flower-visiting bees, invasive plants, *Melilotus*, native plants, *Tamarix*

INTRODUCTION

Invasive plant species have become a major environmental problem on North American rangelands and wildlands (DiTomaso 2000; Duncan et al. 2005). U.S. National Park Service lands managed to preserve native ecosystems are not exempt from this invasion (Benjamin and Hiebert 2004). As of July 2006, over 600 alien plant species had been recorded from U.S. National Parks and Monuments (National Park Service 2006) even though "most parks lack complete weed inventories" (National Park Service 2006).

Many of these alien plant species, originally introduced to North America for beneficial reasons, have subsequently attained weed status (DiTomaso 2000; Duncan et al. 2005). One example is *Tamarix*, a hybrid complex of eight to twelve species introduced to the United States for erosion control and shade beginning in the 19th century (Gaskin and Schaal 2002). Subsequently, some would argue *Tamarix* has become a transformer species (Richardson et al. 2000b) of riparian habitats in the western United States (DiTomaso 1998); others see it as a colonizer of previously modified habitat (Anderson 1998; Glenn and Nagler 2005; Shafroth et al. 2005). Other examples are yellow and white sweet clover, *Melilotus* spp., which probably found favor as a pasture plant in the 17th century (Turkington et al. 1978). *Melilotus,* too, is adjudged a weed under certain circumstances (Turkington et al. 1978.). Both *Tamarix* and *Melilotus* occur in several National Parks and Monuments in the western U.S. (National Park Service 2006). (Authority names for all taxa given in Table 1 (plants) or the Appendix (bees)).

One of the many reasons cited for the weed status of *Tamarix* is its succession of native woody species in riparian habitat and its oft-cited negative effect on native wildlife abundance and diversity (DiTomaso 2000; Shafroth et al. 2005). For example, in their review, Shafroth et al. (2005) reported that many bird species and all members of the herpetofauna were less abundant or diverse in *Tamarix* stands than in other riparian vegetation types (e.g., willow (*Salix* sp.), cottonwood (*Populus* sp.)).

Comparisons of insect abundance and diversity between *Tamarix* and other vegetation types have tended to focus on insects as prey items; results have been quite disparate (refs., Shafroth et al. 2005). For example, Ellis et al. (2000) found little difference between *Tamarix* and *Populus* in surface-active arthropods; Yard et al. (2004) found some insect taxa more abundant in *Tamarix* stands but that, overall, abundance and diversity was higher in mesquite (*Prosopis)*-acacia (*Acacia)* stands; Anderson et al. (2004) compared insects in six vegetation types and found no evidence for a depauperate fauna in *Tamarix*. Drost et al. (2003) and Durst (2004), using Southwestern Willow Flycatcher (*Empidonax traillii extimus*) diet as an indication of insect fauna, showed significant differences in diets between *Tamarix* and willow habitats. However,

Table 1. Plant taxa (abbreviations in parenthesis) and sites of bee collection in Capitol Reef National Park, 2003. Also shown are dates of collection in July, the number of time periods collections were made, the units collected from (F=flowers, H=heads, I=inflorescences, P=plants) and total minutes of collection. SC = Sulphur Creek, PC = Pleasant Creek, FR = Fremont River.

Species	Site	Days	Periods	Units	Minutes
Castilleja exilis A. Nels. (CaEx)	SC	11, 18, 26, 31	10	330-380 I	180
Melilotus albus Desr. Ex Lam. (MeAl)	SC	11, 18, 26, 31	10	30-75 P	165
Tamarix spp. L. (Tamar)	SC	18, 26, 31	9	30-80 I	135
Castilleja linariifolia Benth. (CaLi)	PC	25, 30	6	50-55 I	90
Cleome lutea Hook. (ClLu)	PC	16, 17, 25, 30	8	20-25 P	120
Melilotus officinalis (L.) Pallas (MeOf)	PC	17, 25, 30	7	25-100 P	105
Oenothera pallida Lindl. (OePa)	PC	25, 30	3	145-170 F	45
Orobanche ludoviciana Nutt. (OrLu)	PC	17, 25, 30	7	10-40 P	105
Senecio spartioides T. & G. (SeSp)	PC	25, 30	5	200 H	75
Solidago canadensis L. (SoCa)	FR	23	2	25 I	45
Tamarix spp. L. (Tamar)	FR	23	3	90 I	60

Durst (2004) found no difference in actual arthropod abundance between *Tamarix* and willow habitats.

There have been few studies of the diversity of beneficial insects, such as pollinators, on the flowers of widespread aliens such as *Tamarix* and *Melilotus* in invasive settings. An exception is Nelson and Anderson (1999) who found that butterflies were more diverse in "natural" areas than in *Tamarix*; nevertheless, *Tamarix* supported 16 species in an area less than 10% of that covered by "natural" habitat, which supported 34 species. Here we focus on another beneficial group: native bees (Apiformes). As the most important pollinators of native plants, bees are essential species in most native ecosystems. Many species specialize on the pollen (rarely nectar) of particular plant taxa (Cane and Sipes 2006; Minckley and Roulston 2006). Bees are known to find flowers of both *Tamarix* and *Melilotus* attractive (Bohart 1960; Shmida 1991; Free 1993). If bees are lured away from visiting native plants by invasives, natives could experience declines in fruit and seed production and, eventually, in recruitment (e.g., Grabas and Laverty 1999; Brown and Mitchell 2001; Chittka and Schürkens 2001; Brown et al. 2002; Moragues and Traveset 2005; Totland et al. 2006).

Our study shares several objectives with that of Memmott and Waser (2002): (1) How many bee species are associated with the flowers of invasive *Tamarix* and *Melilotus* and native co-flowering plants during a brief period of mid-summer flowering? (2) Are invasives visited by bee species that normally visit closely related plants or by bees that have generalized foraging habits? (3) Are bees collecting pollen and nectar of invasives? and (4) Are invasives competing with native plants for pollinators?

METHODS

We used an insect net to capture flower-visiting bees from ten co-blooming plant taxa (Table 1) in Capitol Reef National Park, Wayne Co. Utah, on nine warm, clear days from 11-31 July 2003 at three riparian sites: Sulfur Creek (SC: 1.7 km WNW Fruita, 12S E476802 N4238134); Pleasant Creek (PC: 3.2 km S Eph Hanks Tower, 12S E482783 N4225039); and Fremont River (FR: 6.8 km E Fruita, 12S E485172 N4237365). The seven native plant taxa were chosen for their moderate to high abundance and close proximity to the three blooming invasive species. The vegetation of these sites was described as cottonwood-rabbitbrush (*Chrysothamnus*) woodland community (Romme et al. 1993); see also Heil et al. (1993) for other associated species.

Collections of all flower-visiting bees were made as a collector monitored clumps of flowers of one plant species throughout the day in 15 or 30 minute periods, depending on time available, number of species to be sampled, and the abundance of sampled species. (Sampling time was approximately related to species abundance). We sampled each of several plant species at different times throughout most days by alternating between nearby clumps at the same site. Depending on the plant taxon, we either sampled flower stalks, inflorescences, heads, or whole flowers or plants. Table 1 shows the sites, dates and numbers, and types of flowering units sampled for each taxon.

Captured bees were transferred to a cyanide-killing vial and pinned later. They were returned to the USDA ARS Bee Lab, Logan, Utah, for identification. For analysis, we pooled collection data across dates for each plant species because we were primarily interested in overall patterns of association.

Pollen carried in the "pollen baskets" of female bees gives an indication of plant species visited during the current foraging trip. We sampled and identified pollen carried by females visiting *Tamarix* and *Melilotus* using methods described by Beattie (1971). Several hundred pollen grains from each bee were examined in multiple transects across each prepared pollen slide under a compound microscope at 400X. Pollen was compared with our pollen reference collection and scored as *Tamarix*, *Melilotus,* or other.

RESULTS

Invasive plant species had as many or more associated bee species and individuals as did native plant species. During 1125 total minutes of collection (465 min from exotics) on nine days (Table 1), we collected 54 bee species (Appendix), 20 on native plants, 19 on invasives, and 15 on both (Table 2). On average, 15.7 (standard deviation 2.9) bee species were associated with invasive plant species and only 6.9 (sd 5.2) with native plant species. Five plant species were visited by > 10 bee taxa; three of these were invasive plant species (Table 2): in order of decreasing bee taxa, these were *Melilotus albus, Cleome lutea, Tamarix, M. officinalis,* and *Castilleja liniariifolia*. Four of these same five also had the most bee individuals visiting them, though not in the same order.

Using the proportion of time spent collecting from native (58.7%) and invasive (41.3%) plant species

Table 2. Number of individuals of abundant bee species collected on seven native and three invasive plant species in 2003 at Capitol Reef National Park. Uncommon species are grouped by family: Andr = Andrenidae; Apid = Apidae; Coll = Colletidae; Hali = Halictidae; Mega = Megachilidae. Bee species abbreviations refer to Appendix; Numbers in parenthesis are the number of uncommon species; #NA and #IN are the number of individuals of each bee taxon collected on native and invasive plants, respectively. Plant species abbreviations refer to Table 1.

	SULPHUR CREEK			FREMONT		PLEASANT CREEK						TOTALS	
BEE TAXA	**CaEx**	**MeAl**	**Tamar**	**Tamar**	**SoCa**	**CaLi**	**ClLu**	**OePa**	**OrLu**	**SeSp**	**MeOf**	**#NA**	**#IN**
PeCa		69	4	1			6			1		7	74
PeSu		2	12		21		3			12		36	14
PeZe							154			5		159	
Misc Andr (5)		2	1		2		6			1		9	3
Misc Apid (10)		3	2	5			5				6	5	16
CoPe		29					4				16	4	45
CoSl		1	2	4							7		14
Misc Coll (5)		3	3				1			2		3	6
LaCm			18										18
LaOv	8					3					1	11	1
LaTe	2	1	12			4	1					7	13
Misc Hali (14)	1	2	2	2	1	8	12	3		1	3	26	9
MePr		5	4	2			1					1	11
MeSu											12		12
Misc Mega (10)		9	2			5	3		12	6	5	26	16
Total inds	11	126	62	14	24	20	196	3	12	28	50	294	252
Bee Taxa (54)	3	19	13	6	3	11	16	3	3	9	14		

and assuming equal attraction of bees to native and invasive plants, we expected 320 individuals on natives and 226 on invasives. When we compared these expectations with the actual collections using contingency tables (Maxwell 1961), native plant species (294 individuals) proved significantly less attractive than invasives (252 individuals; $X^2 = 5.1$, df = 1, $P < 0.05$). Overall, male and female bees were distributed in the same proportion across invasive and native plant species ($X^2 = 1.62$, df = 1, $P > 0.10$), suggesting that visits to invasives were not primarily due to the less discriminatory nectar foraging behavior of male bees (Baker and Hurd 1968).

We tallied 10 "common" bee species (≥ 10 inds; Table 2). Common species tended to visit several plant species. Six common bee species visited both native and invasive plant species; one was captured only on native plants and three only on invasive plants. Three bee species visited primarily native plants (between 72-100% of visits), while seven visited mostly invasive species (between 65-100% of visits). Bee species that visited invasive plants visited an average of 3.1 (sd 1.4) plant species; those that visited native plants visited an average of 3.6 (sd 1.1) plant species.

For the most part, invasives attracted generalist bee species. Six of seven common bee species visiting invasives are known to be polylectic (i.e., opportunistic flower-visitors which tend to collect a variety of pollens) (Krombein et al. 1979; Table 2). The only exception was *Colletes petalostemonis*, a frequent (91.8%) visitor of *Melilotus* flowers that usually prefers native legumes (Krombein et al. 1979; V. Tepedino, unpubl. data). In contrast, all three abundant bee species visiting native plants were probably pollen specialists (Krombein et al. 1979): *Perdita zebrata* (*Cleome*), *Perdita subfasciata* (Asteraceae), and possibly *Lasioglossum ovaliceps* (Scrophulariaceae) (V. Tepedino, unpubl. data).

Five common species of bees were represented by ≥ 5 females on *Tamarix* flowers (Tables 2, 3). Most of the females of four of these species were carrying pollen in their scopa (Table 3); females of the fifth species, *Perdita subfasciata* (PeSu), were collecting only nectar. The pollen loads of females of three species were virtually pure *Tamarix*; that of one species, *Megachile prosopodis* (MePr), was about half *Tamarix* pollen.

We also scored the pollen-collecting behavior of *Colletes petalostemonis* (CoPe), the lone legume specialist captured on *Melilotus* flowers: 36 of 43 females were collecting pollen. Of these, 28 had appreciable pollen in their scopa. We randomly selected ten of these 28 females and identified the pollen carried in their scopa. All ten carried only *Melilotus* pollen.

DISCUSSION

Unquestionably, invasive plants such as *Tamarix* and *Melilotus* can effect native bee populations, the native plants those bees service, and the ecosystems they anchor. The details of those effects, however, are likely to be complicated by factors such as site characteristics and plant associations. Such complications illustrate that simplistic approaches and assumptions are likely of little value to resource managers and others engaged in the invasive issue. It will be a very rare invasive that is "totally bad" for an ecosystem.

Our findings support the contention of Richardson et al. (2000a) that invasive species are unlikely to suffer from pollinator inattention. We recorded as many species of bees visiting the flowers of invasives as visiting natives (Table 2). On average, over twice as many bee species were associated with the three invasive species as with the seven native taxa. Thus, the spread of invasives that offer pollen and nectar, and are at least partially dependent on pollinators for sexual reproduction like *Tamarix* (Stevens 1989; Shmida 1991) and *Melilotus* (Bohart 1960; Sano 1977), is likely to be facilitated by native pollinators.

These results contrast with the analysis of data from Illinois, 1895-1916 (Robertson 1929), by Memmott and Waser (2002) who found significantly more flower visitor species associated with native plants than with invasives. The difference between studies may be due to: (1) the inclusion of all flower-visiting insects by Memmott and Waser (2002) (whereas we dealt only with bees); (2) the obscuring of details by lumping data from all years (Robertson 1929); or (3) the fact that Robertson's (1929) data is from a much earlier stage of invasion (many of those invasives were thought to be uncommon (Memmott and Waser 2002); ours were abundant and probably more attractive).

Richardson et al. (2000a) and Memmott and Waser (2002) also concluded that most of the insects that visit the flowers of abundant invasives are generalists. We too found that, with one exception, the common

Table 3. Purity of pollen loads of abundant female bee species captured on *Tamarix* or *Melilotus* flowers in 2003 in Capitol Reef National Park. #♀♀ is the total number of females caught, #Pollen is the number of females with pollen, % is the average (SD) purity of the pollen load. Bee abbreviations refer to the Appendix.

Species	#♀♀	#Pollen	%
		Tamarix	
CoSl	5	4	100
LaCl	18	13	89.8 (30.9)
LaTe	12	10	99.8 (45.7)
MePr	6	6	51.3 (47.9)
PeSu	8	0	–
		Melilotus	
CoPe	10	10	100

bees that visited *Tamarix* and *Melilotus* during our three weeks of collections were generalists. Other contemporaneously flying specialists (e.g., the *Cleome* specialist *Perdita zebrata flaven*s and the composite specialists *Megachile parallela* and *Melissodes utahensis* (Appendix), common on *Grindelia squarrosa,* and *Helianthus annuus* in other contemporaneous collections) were not drawn to invasives from their host plants. The expectation that specialist bees are more likely to visit flowers of invasive plants closely related to their native host taxa was testable only for *Melilotus* (*Tamarix* has no close relatives in the Park). The only legume specialist we recorded, *Colletes petalostemonis*, was abundant on the flowers of both species of *Melilotus* (Table 2).

Protein and lipid rich pollen is the primary source of nutrients provided by adult female bees to their offspring (Roulston and Cane 2000; Roulston *et al*. 2000). In general, the bee species that commonly visited *Tamarix* and *Melilotus* flowers collected pollen as well as nectar (Table 3), suggesting that they used this to provision their cells and rear progeny. If *Tamarix* pollen is of sufficient nutritional value to support maturation of immature bees to adults, then it may constitute a recently added "cornucopian" resource (Mosquin 1971) with the potential to support the production of many native bees; *Melilotus* pollen is already suspected to be so constituted (Bohart 1960; Sano 1977).

The attraction of pollinators to invasive plants may have facilitative or competitive effects on co-blooming native plant species (Rathcke 1983; see below). For example, *Melilotus* might either be facilitating the reproduction of native host plants such as *Petalostemon* or *Psoralea* or repressing it through competition for pollinators like the legume specialist *C. petalostemonis* (Rathcke 1983). Facilitation appears to be uncommon, the conditions allowing it restrictive (Feldman et al. 2004; Moragues and Traveset 2005); evidence for competitive effects are more usual (Grabas and Laverty 1999; Chittka and Schürkens 2001), including one example of intragenus competition (Brown and Mitchell 2001; Brown *et al*. 2002). However, not all studies purporting to show competition show a decline in seed production by native species (Larson et al. 2006; Totland et al. 2006). Competition for pollinators during our study is unlikely because few flower species were in bloom and many bee species in flight; it is more likely at other times of the year when pollinators are more in demand.

Finally, with respect to native bees, invasive plants such as *Melilotus* and *Tamarix* may not deserve their reputation as environmental scourges because, over time, they have actually increased native bee carrying capacity and population size by providing additional nectar and pollen when "natural" supplies are low. Mid to late July in Capitol Reef National Park, as in other areas of the western U.S., is a time of reduced floral diversity and few flowers. In addition to the native plant species reported here, we detected only *Grindelia squarrosa* and *Helianthus annuus* in appreciable bloom at other nearby sites. Thus, *Melilotus* and *Tamarix* may be filling a mid-summer gap in floral resources for native bees.

Bees that would benefit from such a floral flush are older females that have outlived the bloom of their host plants and young females of other species that have emerged before the bloom of their host plants. The pollen and nectar of invasives might then: (1) allow older females to continue producing offspring; (2) enable young females to begin reproducing early (and perhaps begin adapting to a new host), or (3) maintain all females until the next acceptable native plant blooms (Waser and Real 1979), at which time they can resume producing offspring. The latter is unlikely, at least for older females, because individuals of most native solitary species are short-lived; they fly for only a few weeks. It is scenarios 1 and 2 that are more likely. In either case, population numbers of native bees are likely to increase in size during the course of invasion by an entomophilous alien, until a new, loose equilibrium between floral resources and bees is reached.

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Appendix A. Bee species captured from native and exotic plant species in Capitol Reef National Park, 2003, grouped by family. Abbreviations for Table 2 in parentheses.

<u>Andrenidae (8)</u>: *Andrena prunorum prunorum* Cockerell (AnPr), *Perdita* n.sp. aff. *zebrata* (PeAfZe), *P. albipennis* Cresson (PeAl), *P. aridella* Timberlake (PeAr), *P. calloleuca* Cockerell (PeCa), *P. subfasciata* Cockerell (PeSu), *P. zebrata flavens* Timberlake (PeZe), *Protandrena (Heterosarus)* n.sp. (PrHe).

<u>Apidae (10)</u>: *Anthophora urbana urbana* Cresson (AnUr), *Apis mellifera* Linnaeus (ApMe), *Bombus morrisoni* Cresson (Bomo), *B. pennsylvanicus* (DeGeer) (BoPe), *Diadasia diminuta* (Cresson) (DiDi), *Melissodes* sp. CR1 (MeC1), *M. utahensis* LaBerge (MeUt), *Neolarra* sp. (NeSp), *Nomada* sp. CR3 (NoC3), *Triepeolus* sp. CR2 (TrC2).

<u>Colletidae (7)</u>: *Colletes petalostemonis* Swenk (CoPe), *C. simulans nevadensis* Swenk (CoSi), *C. slevini* Cockerell (CoSl), *Hylaeus* aff. *cookii* n.sp. (HyAfCo), *H. bisinuatus* Forster (HyBi), *H. megalotis* (Swenk & Cockerell) (HyMg), *H. mesillae cressoni* (Cockerell) (HyMc).

<u>Halictidae (17)</u>: *Agapostemon angelicus* Cockerell /*texanus* Cresson (AgAn), *A. melliventris* Cresson (AgMe), *Halictus ligatus* Say (HaLi), *H. tripartitus* Cockerell (HaTr), *L. clarissimus* (Ellis) (LaCr), *L. clematisellus* (Cockerell) (LaCm), *L. ovaliceps* (Cockerell) (LaOv), *L. tegulariformis* (Crawford) (LaTe), *Lasioglossum (Dialictus)* sp. 1,3,4,5,6,7,8,9 (LaS1, 3-9), *L* . sp. E7 (LaE7).

<u>Megachilidae (12)</u>: *Anthidiellum notatum robertsoni* (Cockerell) (AnNo), *Ashmeadiella bucconis* (Say) (AsBu), *A. cactorum* (Cockerell) (AsCa), *Coelioxys hunteri* Crawford (CoHu), *Dianthidium parvum* (Cresson) (DiPa), *D. pudicum* (Cresson) (DiPu), *Megachile (Litomegachile)* sp. (MeLi), *M. inimica* Cresson (MeIn), *M. lippiae* Cockerell (MeLi), *M. parallela* Smith (MePa), *M. prosopidis* Cockerell (MePr), *M. subexilis* Cockerell (MeSu)